

ALLOZYME PHYLOGENY OF NORTH AMERICAN COPPERS (LYCAENINAE: LYCAENIDAE)

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Abstract.—Phylogenies were created with allozyme data of 15 species and two subspecies of North American coppers. Most of the species align with the currently recognized subgenera of the subfamily Lycaeninae. These subgenera exhibit a significant level of genetic differentiation that is perhaps equivalent to genera. The subgenus *Epidemia* unexpectedly includes *Lycaena hyllus* (Cramer), which is currently assigned to a separate monotypic subgenus. The Nei Distance tree separates the North American taxa into two distinct biological groups. One group diapauses as partially grown larvae and has its closest relatives in the Palearctic based on morphological data. The other group is endemic and diapauses in the egg stage (first instars within eggs). Divergence within the Distance Wagner tree parallels unique host shifts that have occurred several times in the North American coppers. Most shifts have originated from a *Rumex* feeding species. The host shift to *Eriogonum* has produced at least two and possibly more species. A few species have adapted to *Vaccinium*; these shifts appear to have occurred independently.

Key Words.—Insecta, *Lycaena*, *Epidemia*, Lycaeninae, host shifts, diapause.

The taxonomy of the North American coppers (subfamily Lycaeninae) has a complex history. In the past two centuries, the species have been classified under several lycaenid genera such as *Polyommatus* Latreille, *Lycaena* Fabricius, *Chrysophanus* Hübner, and *Heodes* Dalman. Miller & Brown (1979) in an attempt to balance taxonomy with a proposed copper phylogeny resurrected genera originally named by Scudder in 1876 (*Tharsalea*, *Chalceria*, *Gaeides*, and *Epidemia*) and also erected monotypic genera (*Hyllolycaena* and *Hermelycaena*) for the species *Lycaena hyllus* and *L. hermes* (W. H. Edwards) respectively. Their subsequent systematic catalogue followed the same trend using a total of seven genera (Miller & Brown 1981). However, a recent checklist of California butterflies conservatively placed all coppers in the genus *Lycaena* with further division provided by the subgenera *Lycaena*, *Epidemia*, *Chalceria*, *Hermelycaena*, and *Tharsalea* (Emmel et al. 1998). These authors did not recognize the subgenus *Gaeides*, because its type species is closely related to the type species of *Chalceria*. *Chalceria* has page priority over *Gaeides* in Scudder (1876).

Miller & Brown (1979) pointed out the primitive features of *Lycaena phlaeas* and *L. cuprea* and speculated on their probable origin in the Palearctic. The source of North American *L. phlaeas* populations is uncertain, but *L. phlaeas* has many subspecies throughout the Old World, several of which could have served as founders. Regarding *L. cuprea*, Klots (1936) and Sibatani (1974) independently noted a kinship between this North American species and the Eurasian species *L. alciphron* (Rottemburg). Strong similarities exist between these two species in both genitalia and facies. While it is tempting to link *L. cuprea* with *L. alciphron* in a unique Palearctic genus, the proper generic assignment of *alciphron* is presently uncertain. Modern workers have variably placed it in *Heodes*, *Lycaena*, and

Thersamonolycaena (Higgins 1975, Higgins & Riley 1983, Korshunov & Gorbunov 1995, Tolman 1997, Tusov 2000, Gorbunov 2001). Also of great interest are recently discovered, high altitude Asian species, which display even stronger similarities to *L. cuprea* (Wyatt 1961, Churkin 1999). New studies are needed to resolve the relationship of *L. cuprea* with Palaearctic genera.

Coppers as a whole have a worldwide distribution indicating these butterflies may belong to a very old lineage (Lewis 1973, Miller & Brown 1979). It has been suggested that their earliest divergence began before the continental separation of Pangaea in Late Cretaceous (Miller & Brown 1979). Their distribution presently extends from Eurasia to South Africa, from Asia to New Zealand (including Malayan Peninsula and Papuan region), and from North America to Central America where a single species, *Lycaena (lophanus) pyrrhias* (Godman & Salvin), resides in high elevation cloud forests. They are absent throughout South America and Australia (Clark & Dickson 1971, Miller & Brown 1979, Gibbs 1980, Higgins & Riley 1983, Korshunov & Gorbunov 1995, Gorbunov 2001).

Copper larvae throughout the world, with the exception of North America, feed exclusively on plants in the family Polygonaceae. They chiefly utilize closely related members of the genera *Rumex*, *Polygonum*, and *Muehlenbeckia*. In North America several coppers have shifted onto unique non-polygonaceous hosts, including *Rhamnus* (Rhamnaceae), *Eriogonum* (Polygonaceae), *Ribes* (Grossulariaceae), *Vaccinium* (Ericaceae), and *Potentilla* (Rosaceae) species. Determining what factors caused these butterflies to make host shifts is essential to understanding their evolution.

In this study we produced phylogenies using allozyme analyses of 15 species of North American coppers. We surveyed the various trees for species clusters and compared these clusters for taxonomic congruence with the currently known taxa of the Lycaeninae. We also compared life history features and speculated how some North American coppers may have evolved through diapause changes and host shifts.

MATERIALS and METHODS

Enzyme Analysis.—Fresh or frozen butterflies were homogenized, electrophoresed on 10% starch gels, stained for enzymes, and scored following the procedure of Pratt (1994). The butterfly sample sizes and sites of collection are shown in Table 1. They were stored at -70°C . After removal of the wings the remainders were homogenized in 50 μl of buffer (0.005 M Tris-HCl pH 7.5) per butterfly. The homogenates were stored in microtiter plates at -70°C and electrophoresed on gels with a citrate-aminopropyl-morpholine continuous system (pH 8.5) (Clayton & Tretiak 1972). The enzymes aconitase (ACO-1 & ACO-2), adenylate kinase (AK-1 & AK-2), aspartate amino transferase (AAT-1 & AAT-2), alpha glycerophosphate dehydrogenase (αGPD), glucose phosphate isomerase (GPI), glucose-6-phosphate dehydrogenase (G6PD), hexokinase (HEX-1 & HEX-2), isocitrate dehydrogenase (IDH-1 & IDH-2), malic dehydrogenase (MDH-1 & MDH-2), malic enzyme (ME-1), peptidase [leucyl-glycyl-glycine (PEP-1 & PEP-2) as a substrate], phosphoglucomutase (PGM), and superoxide dismutase (SOD-1, SOD-2, SOD-3) were stained with conventional histochemical stains (Shaw & Prasad 1970). Alleles were scored by distance from the origin.

Analysis of Allelic Variation.—The allelic variations of the 22 presumptive loci

Table 1. Sample sizes and locations of *Lycaena* populations used for enzyme analysis.

Subgenus	Species	N	Location
<i>Chalceria</i>	<i>rubida</i>	8	Bridgeport CA
	<i>xanthoides</i>	3	Southern CA
	<i>editha</i>	8	E Sierra Nevada, CA
	<i>dione</i>	8	Lincoln, Nebraska
	<i>gorgon</i>	8	Frazier Park, CA
	<i>heteronea</i>	8	White Mts., CA
<i>Epidemia</i>	<i>helloides</i>	8	Olancho, CA
	<i>nivalis</i>	13	Sonora Pass, CA
	<i>mariposa</i>	8	Cedar Lake, CA
	<i>epixanthe</i>	5	Chatsworth, NJ
<i>Hyllolycaena</i>	<i>hyllus</i>	9	Ravenwood, MD
<i>Tharsalea</i>	<i>arota arota</i>	6	San Gabriel Mts., CA
	<i>arota nubila</i>	4	Santa Monica Mts., CA
<i>Hermelycaena</i>	<i>hermes</i>	3	San Diego Co., CA
<i>Lycaena</i>	<i>phlaeas</i>	10	Newark, DE
	<i>cuprea</i>	2	Donner Pass, CA

were analyzed as individual genotype data by BIOSYS-1 (Swofford & Selander 1989). Numerous genetic distances (Nei, Nei unbiased, Nei minimum, Nei unbiased minimum, Nei identities, Nei unbiased identities, Rogers, Modified Rogers, Prevosti, Cavalli-Sforza & Edwards chord, Cavalli-Sforza & Edwards arc, and Edwards "E") were produced by BIOSYS-1. Cluster analyses were performed by the method of Sneath and Sokal (1973) using the genetic distances and the following algorithms: unweighted pair-group method with arithmetic averaging (UPGMA), weighted pair-group method with arithmetic averaging (WPGMA), single linkage (SL), and complete linkage (CL). Distance Wagner trees, utilizing the multiple addition criterion algorithm of Swofford (1981), were produced by midpoint rooting with Rogers, Modified Rogers, Prevosti, Cavalli-Sforza & Edwards chord, Cavalli-Sforza & Edwards arc, and Edwards "E" distances (Parris 1972).

RESULTS

The mean number of alleles per locus, percent polymorphic loci, and heterozygosity of North American copper species are shown in Table 2. (A copy of allele frequencies is available upon request.) The mean number of alleles per locus and percent polymorphic loci ranged from 1.1 to 6.7 and 9.1 to 54.5, respectively (Table 2).

Many cluster analysis trees were produced using algorithms and various genetic distances. Trees with the highest cophenetic correlation and lowest standard deviation were identical in topology to the UPGMA tree created with Nei distances (Fig. 1). The Nei Distance tree groups most species into their currently recognized higher taxa. The species *L. rubida* (Behr), *L. xanthoides* (Boisduval), *L. editha* (Mead), *L. dione* (Scudder), *L. gorgon* (Boisduval), and *L. heteronea* Boisduval cluster in the subgenus *Chalceria*. Allied species *L. gorgon* and *L. heteronea* from a distinct separate cluster within *Chalceria*. The species *L. epixanthe* (Boisduval & Le Conte), *L. hyllus*, *L. helloides* (Boisduval) *L. mariposa* (Reakirt), and *L.*

Table 2. Mean number of alleles per locus, percent polymorphic loci, and heterozygosity.

Population	Mean no. of alleles per locus	Mean % of loci polymorphic*	Heterozygosity	
			Direct count	H-W expected**
<i>rubida</i>	1.4 (0.1)	27.3	0.124 (0.049)	0.109 (0.042)
<i>xanthoides</i>	1.2 (0.1)	13.6	0.045 (0.033)	0.079 (0.043)
<i>editha</i>	6.7 (0.2)	50.0	0.195 (0.058)	0.170 (0.046)
<i>dione</i>	1.6 (0.1)	54.5	0.239 (0.064)	0.197 (0.049)
<i>gorgon</i>	6.6 (0.2)	50.0	0.186 (0.052)	0.164 (0.042)
<i>heteronea</i>	6.6 (0.2)	31.8	0.157 (0.061)	0.132 (0.049)
<i>helloides</i>	6.6 (0.2)	40.9	0.146 (0.044)	0.135 (0.040)
<i>nivalis</i>	3.0 (0.0)	18.2	0.076 (0.038)	0.070 (0.033)
<i>mariposa</i>	6.6 (0.2)	45.5	0.102 (0.030)	0.100 (0.030)
<i>epixanthe</i>	1.4 (0.1)	27.3	0.127 (0.048)	0.118 (0.045)
<i>hyllus</i>	1.5 (0.2)	31.8	0.095 (0.035)	0.105 (0.039)
<i>arota arota</i>	1.3 (0.2)	22.7	0.106 (0.045)	0.107 (0.046)
<i>arota nubila</i>	1.3 (0.1)	31.8	0.140 (0.054)	0.138 (0.048)
<i>hermes</i>	1.1 (0.1)	9.1	0.030 (0.021)	0.042 (0.031)
<i>phlaeas</i>	1.5 (0.1)	40.9	0.141 (0.050)	0.116 (0.037)
<i>cuprea</i>	1.3 (0.1)	31.8	0.174 (0.062)	0.174 (0.061)

* A locus is considered polymorphic, if more than one allele was detected.
** Unbiased estimate.

nivalis (Boisduval) cluster in the subgenus *Epidemia*. The species *L. arota* (Boisduval) and *L. hermes* cluster together, however they branch below the branching points of other subgeneric groups suggesting they belong to separate subgenera. *Lycaena phlaeas* and *L. cuprea* constitute a cluster that branches basally to all of the above taxa.

Many Distance Wagner Trees were produced by midpoint rooting with various genetic distances. The tree with the highest cophenetic correlation and lowest percent standard deviation was created with Cavalli-Sforza & Edwards arc distances. It is shown in Fig. 2 with host plants added to right in order to facilitate discussion of host shifts. In this phylogeny *Chalceria* again divides into two distinct clusters with *L. gorgon* and *L. heteronea* forming a closely allied pair. The *Epidemia* align in a fashion similar to the Nei Distance tree with a few subtle differences in branching sequence. *Lycaena epixanthe* clusters with *L. hyllus*,

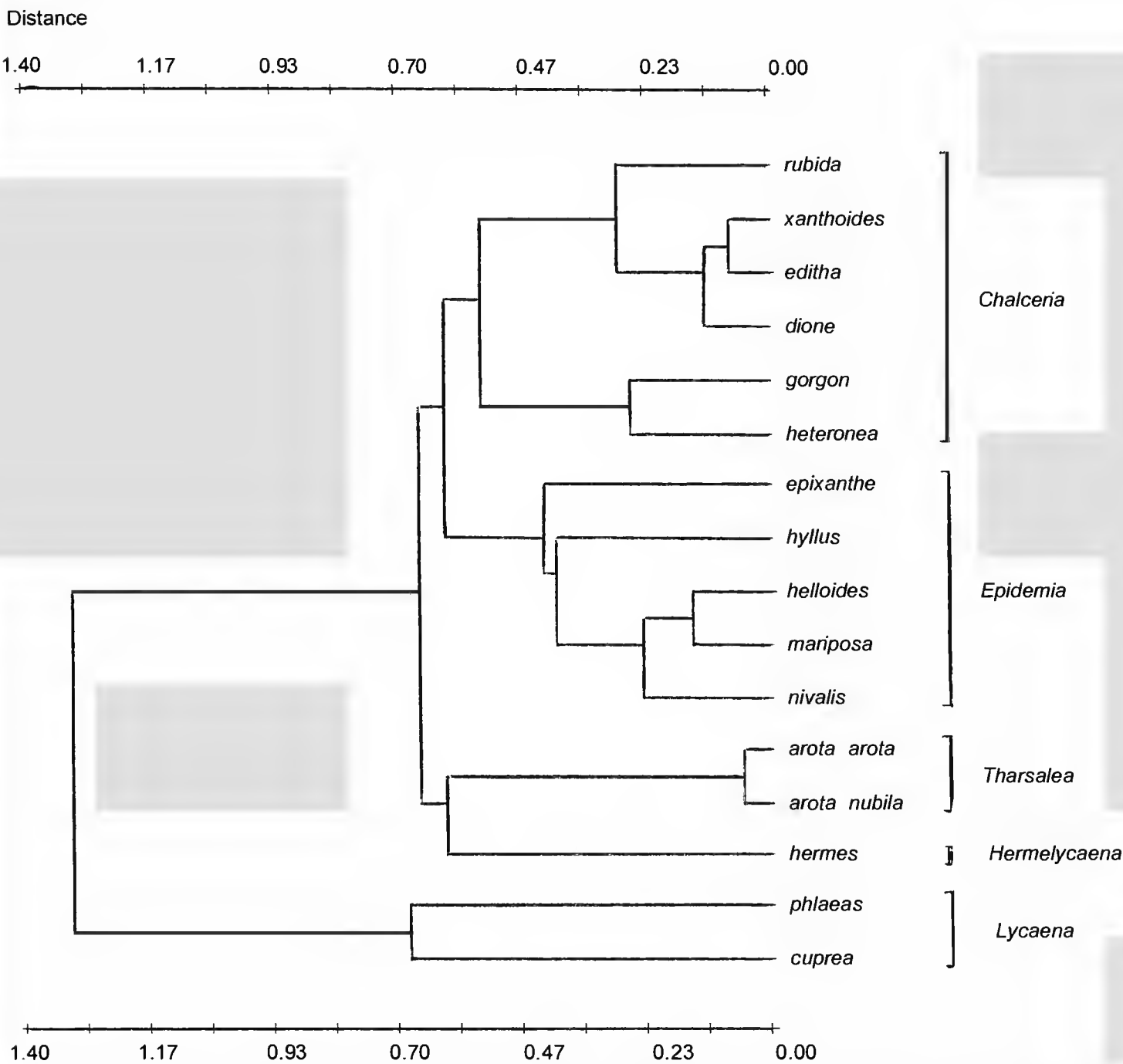


Figure 1. Nei Distance tree. UPGMA tree of 16 North American coppers using Nei distances. Cophenetic correlation 0.925; percent standard deviation 18.896. Subgeneric designations in right margin.

whereas in the Nei Distance tree each species branches independently from the main branch of the group. *Lycaena helloides* clusters with *L. nivalis*, but in the Nei Distance tree it clusters with *L. mariposa*. *Lycaena arota* and *L. hermes* do not cluster together in the Distance Wagner tree. *Lycaena arota* branches from an ancestral stem shared with *Epidemia*, while *L. hermes* branches toward the base of the subfamily just after the *L. phlaeas* and *L. cuprea* branch.

DISCUSSION

Copper Taxonomy.—In our study Nei distances are selected for cluster analysis since they have been used for evolutionary estimates and phylogenies in other arthropods. Despite small sample sizes, which can diminish the overall confidence in results, all of our trees demonstrate regular branching patterns. The trees branch into distinct species clusters with notable levels of genetic differentiation. The topologies of the Nei Distance and Distance Wagner trees (Figs. 1 and 2) show remarkable congruence with the currently recognized North American copper sub-

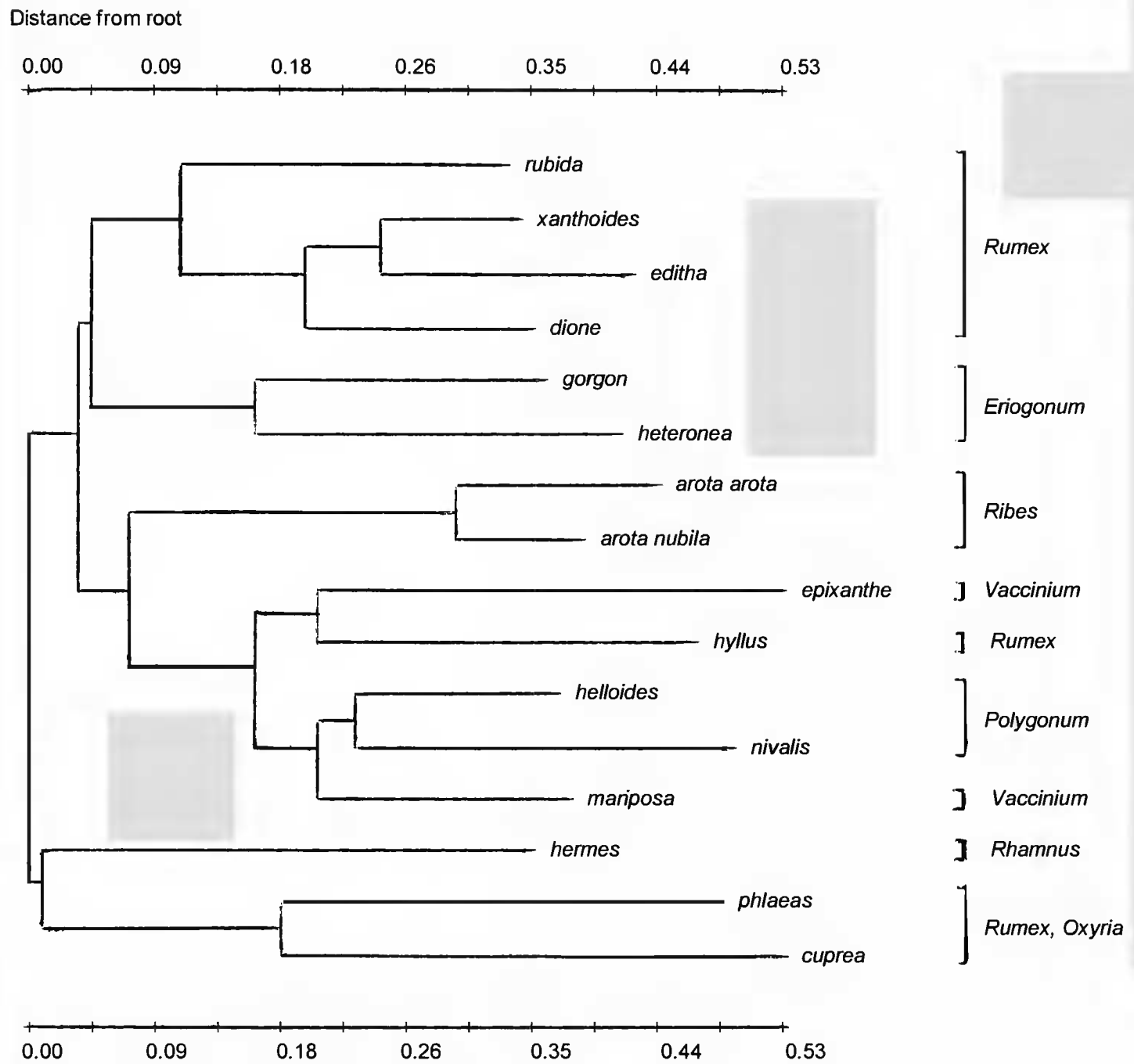


Figure 2. Distance Wagner tree of 16 North American coppers using Cavalli-Sforza & Edwards arc distances. Cophenetic correlation 0.912; percent standard deviation 13.159. Total length of tree = 4.537. Host plants in right margin.

genera. Allozyme differentiation implies that these subgenera are perhaps compatible with genera. Certain copper taxa are absent from the analysis. The addition of *Lycaena ferrisi* K Johnson & Balogh, *L. dorcas* Kirby, *L. cuprea snowi* (W. H. Edwards), and *L. (lophanus) pyrrhias*, as well as larger sample sizes, may improve the trees and disclose further relationships.

Miller & Brown (1979) pointed out the primitive position of *Lycaena phlaeas* and *L. cuprea* relative to other North American taxa. The ancestral position of these species is supported by our allozyme phylogenies. Several subspecies of *L. phlaeas* and many *L. cuprea*-like species occur throughout Eurasia (Henriksen & Kreutzer 1982, Higgins & Riley 1983, Korshunov & Gorbunov 1995, Tusov 2000, Gorbunov 2001). With extant relatives in the Palaearctic, it is most likely that the ancestors of both *L. phlaeas* and *L. cuprea* originated in the Palaearctic.

In our study the population of *Lycaena phlaeas* sampled is from eastern North America. Klots (1951) noted that eastern subspecies *L. phlaeas americana* Harris, corrected to *L. phlaeas hypophlaeas* (Boisduval) by Emmel & Pratt (1998), is

morphologically similar to European *L. phlaeas*. Opler and Krizek (1984) suggested that *hypophlaeas* is adventive and was most likely introduced into North America from Scandinavia during the American Colonial period (17th–18th century). An alternative hypothesis is that eastern populations of *hypophlaeas* existed endemically in the high elevations of the White Mountains in New England and expanded their range with the introduction of *Rumex acetosella*. An expansion of this sort has been observed with alpine populations of *L. cuprea* and *L. editha*. Both of these species have broadened their range with the introduction of *Rumex acetosella* into western North America (Emmel & Pratt, personal observation). Also high altitude California *L. phlaeas* from 12,000 feet elevation can be experimentally reared on *Rumex crispus* at 800 feet elevation (and lower), suggesting that the species has the ability to rapidly adapt to lowland conditions (Ballmer & Pratt 1989a). *Oxyria digyna* is the primary host plant of arctic-alpine *L. phlaeas* in North America (Shields and Montgomery 1966, Ferris 1974, Emmel & Pratt 1998). This plant occurs locally at high elevations on Mount Washington in New Hampshire; the possible existence of high altitude *L. phlaeas* colonies there and elsewhere in New England has not been studied.

Allozyme evidence suggests that each of the four species at the base of the tree (*L. phlaeas*, *L. cuprea*, *L. arota*, *L. hermes*) could belong to a separate genus or subgenus. The genetic distance between *L. phlaeas* and *L. cuprea* in the Nei Distance Tree (Fig. 1) is greater than the basal branch leading to all other subgenera. *Lycaena arota* and *L. hermes* from western North America form a cluster pair in the Nei Distance tree (Fig. 1), but fail to do so in the Distance Wagner Tree (Fig. 2). Thus these species seem to require a different grouping above the species level. If they were placed in separate subgenera, two (*L. arota*, *L. hermes*) would occupy monotypic subgenera. *Lycaena phlaeas* and *L. cuprea* on the other hand belong to a polytypic Holarctic subgenus. The current assignment of *L. cuprea* to the *Lycaena* may change once comparative molecular studies with Palearctic taxa have been completed. *Lycaena phlaeas*, the type species of *Lycaena*, will not change assignment.

In both trees (Figs. 1 and 2), the species in *Chalceria* segregate into two distinct subclusters consisting of *L. rubida*, *L. xanthoides*, *L. editha*, and *L. dione* in one group and *L. gorgon* and *L. heteronea* in the other. The branch length between them in the Nei Distance tree (Fig. 1) is virtually the same as branch lengths of other subgenera. A notable shift in host plants has accompanied this split. The first group uses hosts in the plant genus *Rumex*, while *L. gorgon* and *L. heteronea* have shifted to *Eriogonum*. Ballmer and Pratt (1989b) recognized distinct differences in the larvae of these two groups. If these two groups are eventually recognized as separate genera or subgenera, *Chalceria* must be applied to the former and a new genus must be erected for *L. gorgon* and *L. heteronea*.

In the Nei Distance tree (Fig. 1), the distance between *L. dione* and *L. xanthoides* is greater than that between *L. xanthoides* and *L. editha*. This is consistent with the notion that *L. dione* is a distinct species and supports the recent elevation by Opler and Malikul (1992). Whether *L. xanthoides* and *L. editha* are fully separate species is a controversial subject (Scott 1980, Pratt et al. 1991). In this analysis *L. xanthoides* lies intermediate between *L. editha* and *L. dione*. Although the genetic distance between *L. xanthoides* and *L. editha* is relatively small, *L. editha* tentatively should retain full species status. The allozyme relationships of

this group are congruent with the phylogeny in our previous morphological study of the *L. editha* Complex (Pratt et al. 1991). It should be noted that our allozyme study analyzed only a single population of each species and did not sample intermediate *L. editha* $\times$ *L. xanthoides* populations in northern California. We also did not examine *L. ferrisi*, the purported oldest member of this group. These limitations make it difficult to offer a stronger statement about the species status of *L. editha*.

Most of the species within the subgenus *Epidemia* form a clear cluster with the surprising exception of *L. hyllus*, which is currently assigned to the subgenus *Hyllolycaena*. In the Nei Distance tree (Fig. 1), *L. hyllus* is more closely related to the other *Epidemia* species than is *L. epixanthe*. *Lycaena hyllus* and *L. epixanthe* branch together in the Distance Wagner tree (Fig. 2), implying an ancestral relationship. Comparing their phenotypes, this relationship hardly seems possible. It appears that *L. hyllus* is either a member of *Epidemia* or *L. epixanthe* is a member of *Hyllolycaena*. (Alternatively, *L. epixanthe* could represent a separate monotypic subgenus.) Egg morphology and larval chaetotaxy reveal a close relationship between *L. hyllus* and the *Epidemia* species (Wright, personal observation). Future analyses with the addition of *L. dorcas* may help determine the breadth of *Epidemia* and its potential inclusion of *L. hyllus*.

Diapause Changes.—The first branch in the Nei Distance tree (Fig. 1) demarcates a conspicuous split between the species pair *L. phlaeas* and *L. cuprea* and the remaining North American coppers. This branch is coincident with a significant biological modification in diapause. Both *L. phlaeas* and *L. cuprea* diapause as partially grown larvae, while all other North American coppers diapause in the egg stage, or more accurately as first instars within eggs (Scott 1981, Wright 1983, Pratt & Ballmer 1986). Coppers outside of North America principally diapause as partially grown larvae well beyond the first instar (Clark & Dickson 1971, Gibbs 1980, Henriksen & Kreutzer 1982, Higgins & Riley 1983). These observations suggest that the evolution of the North American species, excluding those with their closest relatives in the Palearctic (*L. phlaeas* and *L. cuprea*), involved a diapause change from partially grown larvae to first instar larvae within eggs.

Most species of this unique group of obligate egg-diapausers are univoltine. One curious exception is *L. hyllus*, which has two broods. Progeny of the first brood of *L. hyllus* develop directly without diapause while the second brood in late summer produces eggs whose first instars enter diapause (Opler & Krizek 1984). Thus the diapause stage of this species is ultimately the same as its North American relatives. The modification of voltinism in *L. hyllus* appears to be a response to habitat, climate, moisture, and host availability. The precise mechanism how this species controls diapause is unknown. It is not clear in which stage multibrooded lowland *L. helloides* diapauses, but we speculate that it too diapauses within eggs like its congeners. This species is univoltine at high altitude where Scott (1986) reported egg hibernation. High altitude California *L. helloides* (> 6000 feet) when reared for three generations without diapause near sea level, entered diapause in late fall within eggs (Pratt, personal observation).

Host Plant Shifts.—It is likely that the original host plant of the North American coppers was *Rumex* or a closely related member of the Polygonaceae. Supporting this conclusion is the observation that coppers worldwide use Polygonaceae spe-

cies almost exclusively. The only continent where coppers venture onto hosts outside of the Polygonaceae is North America. Since North American coppers (excluding subgenus *Lycaena*) are more derived than their Palearctic counterparts, host shifts that occurred on this continent were most likely from Polygonaceae to another plant family. Also each North American subgenus with more than one species contains at least one species that feeds on either *Rumex* or *Polygonum* (Ballmer & Pratt 1989b).

The major host shifts of the North American coppers align with the major branches in the allozyme phylogenies. The first branching stem (subgenus *Lycaena*) in the Distance Wagner Tree (Fig. 2) did not switch hosts, but the following divergence (*L. hermes*) saw a host shift to the plant *Rhamnus crocea* Nuttall in Torrey and Gray (Rhamnaceae). The branching stem of the *Chalceria* did not involve a host shift, but within the subgenus there occurred a split leading to the closely allied pair, *L. gorgon* and *L. heteronea*, which shifted onto *Eriogonum*. Although *Eriogonum* belongs to the Polygonaceae family, the ability to feed on this plant genus may be considered a unique host shift. *Rumex* feeding species of *Chalceria* (*L. rubida*, *L. xanthoides*, *L. editha*, and *L. dione*) will not feed on *Eriogonum* in the lab, and in similar fashion *L. heteronea* and *L. gorgon* larvae will not feed on *Rumex*. The *Rumex* feeding species of *Chalceria* can readily switch between *Rumex* and *Polygonum* (Pratt, personal observation). These observations suggest that the shift to *Eriogonum* is an actual host shift and not easily reversible.

The species diversity of the *Eriogonum* feeders may be greater than presently appreciated. The lineage involving *L. heteronea* may contain two or more species. On the eastern slopes of the Sierra Nevada in western North America occur two sympatric populations of *L. heteronea*, one using *Eriogonum umbellatum* Torrey and the other *Eriogonum nudum* Douglas ex Benthams. Adults and larvae of these two populations differ morphologically and suggest that two species coexist (Pratt et al. 1991). Samples of these populations were not included in this analysis.

The next major divergence in the Distance Wagner Tree (Fig. 2) splits the subgenera *Tharsalea* and *Epidemia*. *Tharsalea* is represented by a single species, which has shifted to exclusive use of *Ribes* (Grossulariaceae). In the subgenus *Epidemia* three species feed on either *Rumex* or *Polygonum* (Polygonaceae), but two species have shifted to *Vaccinium* (Ericaceae) (Wright 1983, Pratt & Ballmer 1986, Scott 1986). It appears that these host shifts, unlike the shift to *Eriogonum*, occurred independently since the two *Vaccinium* feeders are not closely related. The bog species *L. epixanthe* is more closely allied to *L. hyllus*, while *L. mariposa* is more closely related to *L. helloides*. We note with interest that host shifts to plants in Ericaceae have also occurred independently in the polyommatine genera *Agriades*, *Lycaeides*, and *Vacciniina*, especially in species adapted to the bog-like habitats (Scott 1986, Emmel & Emmel 1998). *Lycaena dorcas*, another bog/fen dweller in the *Epidemia*, has shifted to *Potentilla* in the Rosaceae.

ACKNOWLEDGMENT

We sincerely thank the following individuals for their services: Cecilia Pierce and Greg Ballmer helped collect many of the butterflies used in this study; Tom Emmel and John Emmel provided invaluable discussions; Tom Wood of the University of Delaware and Clay Sassaman of the University of California at Riv-

erside generously provided lab space for the electrophoretic analysis; and two anonymous reviewers provided helpful comments for improvements in the manuscript.

LITERATURE CITED

- Ballmer, G. R. & G. F. Pratt. 1989a. Instar number and larval development in *Lycaena phlaeas hypophlaeas* (Boisduval) (Lepidoptera: Lycaenidae). *J. Lep. Soc.*, 43: 59–65.
- Ballmer, G. R. & G. F. Pratt. 1989b. A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California. *J. Res. Lep.*, 27 (1): 1–80.
- Churkin, S. V. 1999. A new species of *Thersamonolycaena* from Tadjikistan (Rhopalocera, Lycaenidae). *Atalanta*, 29 (1/4): 125–129.
- Clark, G. C. & C. G. C. Dickson. 1971. Life histories of the South African lycaenid butterflies. Purnell & Sons, Cape Town. 272 pp.
- Clayton, J. W. & D. N. Tretiak. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. *J. Fish. Res. Board Canada*, 29: 237–251.
- Emmel, J. F. & T. C. Emmel. 1998. A new species of *Agriades* (Lepidoptera: Lycaenidae) from the Sierra Nevada and Trinity Alps of California, and the biology and geographic variation of *Agriades podarce* in California. pp. 287–302. *In* Emmel, T. C. (ed.). *Systematics of western North American butterflies*. Mariposa Press, Gainesville, Florida.
- Emmel, J. F., T. C. Emmel & S. O. Mattoon. 1998. A checklist of the butterflies and skippers of California. pp. 825–836. *In* Emmel, T. C. (ed.). *Systematics of western North American Butterflies*. Mariposa Press, Gainesville, Florida.
- Emmel, J. F. & G. F. Pratt. 1998. New subspecies of Lycaeninae from California and a type locality restriction for *Chrysophanus cupreus* W. H. Edwards (Lepidoptera: Lycaenidae). pp. 661–680. *In* Emmel, T. C. (ed.). *Systematics of western North American butterflies*. Mariposa Press, Gainesville, Florida.
- Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. *Am. Nat.*, 106: 645–668.
- Ferris, C. D. 1974. Distribution of arctic-alpine *Lycaena phlaeas* L. (Lycaenidae) in North America with designation of a new subspecies. *Bull. Allyn Mus.*, 18: 1–13.
- Gibbs, G. W. 1980. New Zealand butterflies. Identification and natural history. Williams Collins Publishers Ltd., Auckland. 207 pp.
- Gorbunov, P. Y. 2001. The butterflies of Russia: classification, genitalia, keys for identification (Lepidoptera: Hesperoidea and Papilionidae). Thesis, Ekaterinburg, 320 pp.
- Henriksen, H. J. & I. Kreutzer. 1982. The butterflies of Scandinavia in nature. Skandinavisk Bogforlag, Odense, Denmark. pp. 215.
- Higgins, L. G. 1975. The classification of European butterflies. William Collins Sons & Co., London. 320 pp.
- Higgins, L. G. & N. D. Riley. 1983. A field guide to the butterflies of Britain and Europe (5th ed.). Collins Clear Type Press, London. 384 pp.
- Klots, A. B. 1936. The interrelationships of the species of the genus *Lycaena* Fabricius (Lepidoptera, Lycaenidae). *Bull. Brooklyn Ent. Soc.*, 31: 154–170.
- Klots, A. B. 1951. A field guide to the butterflies of North America, east of the Great Plains. Houghton Mifflin Company, Boston, Massachusetts. 349 pp.
- Korshunov, Y. & P. Gorbunov. 1995. Butterflies of the Asian part of Russia. [In Russian] Ural University Press, Ekaterinburg. 202 pp.
- Lewis, H. L. 1973. Butterflies of the world. Follett Publishing Company, Chicago, Illinois. 312 pp.
- Miller, L. D. & F. M. Brown. 1979. Studies in the Lycaeninae (Lycaenidae) 4. The higher classification of the American coppers. *Bull. Allyn Mus.*, 51: 1–30.
- Miller, L. D. & F. M. Brown. 1981. A catalogue/checklist of the butterflies of America north of Mexico. *The Lep. Soc.*, Memoir No. 2: 1–280.
- Opler, P. A. & G. O. Krizek. 1984. Butterflies east of the Great Plains. The Johns Hopkins University Press, Baltimore, Maryland. 294 pp.
- Opler, P. A. & V. Malikul (illust.). 1992. A field guide to eastern butterflies. Peterson Field Guide Series. Houghton Mifflin Company, New York. 396 pp.
- Pratt, G. F. 1994. Evolution of *Euphilotes* (Lepidoptera: Lycaenidae) by seasonal and host shifts. *Biol. J. Linn. Soc.*, 51: 387–416.

- Pratt, G. F. & G. R. Ballmer. 1986. Clarification of the larval host plant of *Epidemia mariposa* (Lycaenidae) in Northern California. *J. Lep. Soc.*, 40: 127.
- Pratt, G. F., D. M. Wright & G. R. Ballmer. 1991. Multivariate and phylogenetic analyses of larval and adult characters of the Editha Complex of the genus *Lycaena* (Lepidoptera: Lycaenidae). *J. Res. Lep.*, 30: 175–195.
- Scott, J. A. 1980. Geographic variation in *Lycaena xanthoides*. *J. Res. Lep.* 18: 50–59.
- Scott, J. 1981. Hibernial diapause of North American Papilionoidea and Hesperioidea. *J. Res. Lep.*, 18: 171–200.
- Scott, J. 1986. The butterflies of North America. A natural history and field guide. Stanford University Press, Stanford, California. 584 pp.
- Scudder, S. H. 1876. Synonymic list of the butterflies of North America, north of Mexico. *Bull. Buffalo Soc. Nat. Sciences*, 3: 98–129.
- Shaw, C. R. & R. Prasad. 1970. Starch gel electrophoresis of enzymes: a compilation of recipes. *Biochem. Gen.*, 4: 297–320.
- Shields, O. & J. C. Montgomery. 1966. The distribution and bionomics of arctic-alpine *Lycaena phlaeas* subspecies in North America. *J. Res. Lep.*, 5: 231–242.
- Sibatani, A. 1974. A new genus for two new species of Lycaeninae (s. str.) (Lepidoptera: Lycaenidae) from Papua New Guinea. [Appendix: a tentative scheme of higher classification of Lycaeninae (s.str.) of the world.] *J. Australian Ent. Soc.*, 13: 95–110.
- Sneath, P. H. A. & R. R. Sokal. 1973. Numerical taxonomy; the principles and practice of numerical classification. W. H. Freeman, San Francisco, California. 573 pp.
- Swofford, D. L. 1981. On the utility of the distance Wagner procedure. pp. 25–43. *In* Funk, V. A. & D. R. Brooks (eds.). *Advances in cladistics: proceedings of the first meeting of the Willie Hennig society*. New York Botanical Gardens, New York.
- Swofford, D. L. & R. B. Selander. 1989. BIOSYS-1, a computer program for the analysis of allelic variation in population genetics and biochemical systematics. Illinois Natural History Survey, Champaign, Illinois.
- Tolman, T. 1997. Butterflies of Europe. Princeton University Press, Princeton, New Jersey. 320 pp.
- Tusov, V. K. (ed.) 2000. Guide to the butterflies of Russia and adjacent territories (Lepidoptera, Rhopalocera). Volume 2. Pensoft, Sofia-Moscow. 580 pp.
- Wright, D. M. 1983. Life history and morphology of the immature stages of the bog copper butterfly *Lycaena epixanthe* (Bsd. & Le C.) (Lepidoptera: Lycaenidae). *J. Res. Lep.*, 22: 47–100.
- Wyatt, C. W. 1961. Additions to the Rhopalocera of Afghanistan with descriptions of new species and subspecies. *J. Lep. Soc.*, 15 (1): 1–18.

Received 20 February 2002; Accepted 8 November.